

Ancistrocerus capra (de Saussure, 1857), a Valid Species, Not a Synonym of *A. antilope* (Panzer, 1798) (Hymenoptera: Vespidae: Eumeninae)

ALEXANDER V. FATERYGA,¹ JAMES M. CARPENTER,²
AND VALENTINA V. FATERYGA¹

ABSTRACT

Ancistrocerus capra was described by de Saussure in 1857 from North America and then was synonymized with the Palaearctic *A. antilope* (Panzer, 1798) by Bequaert in 1944. Although these species share a combination of two characters (impunctate and shining metapleuron and lateral surface of the propodeum and a bifurcate apex of the aedeagus) not known in other species of *Ancistrocerus*, they are clearly different in the structure of the clypeus (especially in the male) and the male genitalia (structure of the volsella, general shape of the aedeagus, and the structure of its ventral lobe). Thus, *A. capra* is again recognized as a distinct species in the present contribution. This species is distributed in the United States and Canada while *A. antilope* has a trans-Palaearctic distribution. Two subspecies of *A. antilope* known from North America are synonymized with *A. capra*: *A. antilope navajo* Bequaert, 1925 (new synonymy), and *A. antilope allegrus* Bequaert, 1944 (new synonymy); the taxonomic status of *A. capra spenceri* Bequaert, 1944, remains unclear. Bionomics of *A. antilope* and *A. capra* are similar; particularly, these species share an association with apparently the same species of symbiotic mites, *Kennethiella trisetosa* (Cooreman, 1942) (Sarcoptiformes: Winterschmidtidae), and an unusual mating behavior correlated with this association (first of all, several copulations per pair). A difference, however, exists in the number of generations per year and the sex ratio: *A. antilope* has a single (overwintering) generation with a female-biased sex ratio while *A. capra* has an overwintering generation with a male-biased sex ratio and a summer one with a female-biased sex ratio.

¹ T.I. Vyazemsky Karadag Scientific Station—Nature Reserve of RAS—Branch of A.O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Feodosiya, Russia.

² Division of Invertebrate Zoology, American Museum of Natural History, New York.

INTRODUCTION

Ancistrocerus Wesmael, 1836, is one of the largest genera of the eumenine wasps. With 116 described species, this genus is native to most zoogeographical regions except the Australian (Piekarski et al., 2017). Females of these wasps usually nest in preexisting cavities while some Palaearctic and Nearctic representatives of the genus, such as *A. albophaleratus* (de Saussure, 1855), *A. catskill* (de Saussure, 1852), *A. densepilosellus* Cameron, 1911, *A. japonicus* (von Schulthess, 1908), *A. lutonidus* Bohart, 1974, *A. oviventris* (Wesmael, 1836), and *A. waldenii* (Viereck, 1906), are known to construct aerial mud nests attached to stones (Iwata, 1938; Buck et al., 2008; Olszewski and Fateryga, 2023). Another species, *A. tuberculocephalus* (de Saussure, 1852), is able to enlarge and modify preexisting cavities (Cooper, 1979). Most representatives of the genus *Ancistrocerus*, however, merely divide preexisting cavities into cells with mud partitions. These species are common dwellers of trap nests (Rau and Rau, 1918; Taylor, 1922; Krombein, 1967; Collins and Jennings, 1987; Bonelli, 1989; Budriené et al., 2004; Boesi et al., 2005; Buschini and Woiski, 2008; Budrys et al., 2009; Ivanov et al., 2019; etc.) and some of them are used as model species for study the bionomics of the eumenine wasps (Cooper, 1953, 1955, 1966; Cowan, 1984, 1986; Chapman and Stewart, 1996; Budriené, 2001; Budriené and Budrys, 2005, 2007; Budrys et al., 2010; Budrys and Budriené, 2012; etc.).

Ancistrocerus capra was described by de Saussure (1857) from North America, as a species closely related to the Palaearctic *A. antilope* (Panzer, 1798). Bequaert (1925) confirmed the close relation of these species and finally synonymized them (Bequaert, 1944). He indicated that they share two characters unique for the genus *Ancistrocerus*: impunctate and shining metapleuron and lateral surface of the propodeum and a bifurcate apex of the aedeagus. The synonymy of *A. antilope* with *A. capra* was accepted by subsequent researchers (Bohart, 1951; Krombein, 1979; Buck et al., 2008). Thus, the Nearctic *A. capra* was referred to as *A. antilope* in the entire subsequent literature (Cooper, 1953, 1955, 1966; Medler and Fye, 1956; Krombein, 1967; Longair, 1981; Godfrey and Hilton, 1983; Cowan, 1984, 1986; Cowan and Waldbauer, 1984; Chapman and Stewart, 1996; etc.).

Most “Holarctic” species, which had been known in Vespidae previously, were subsequently proved to be actually pairs of allopatric species. Thus, in the subfamily Vespinae, the Nearctic *Dolichovespula albida* (Sladen, 1918) was reinstated as a good species from the Palaearctic *D. norwegica* (Fabricius, 1781) (Carpenter et al., 2011), *D. arctica* (Rohwer, 1916) from *D. adulterina* (du Buysson, 1905) (Kimsey and Carpenter, 2012), *Vespula alascensis* (Packard, 1870) from *V. vulgaris* (Linnaeus, 1758) (Carpenter and Glare, 2010), *V. infernalis* (de Saussure, 1854) from *V. austriaca* (Panzer, 1799) (Kimsey and Carpenter, 2012), and *V. intermedia* (du Buysson, 1905) from *V. rufa* (Linnaeus, 1758) (Kimsey and Carpenter, 2012). Apart from *A. antilope*, a Holarctic distribution was also reported for the eumenine *Pseudepipona herrichii* (de Saussure, 1856). The latter was, however, recently shown to be a complex of three species: the West-Palaearctic *P. herrichii*, the East-Palaearctic and Nearctic *P. aldrichi* (Fox, 1892) (partially sympatric with *P. herrichii*), and the East-Palaearctic *P. valentinae* Fateryga, 2022 (partially sympatric with *P. aldrichi*) (Fateryga, 2022). These three species are very similar in structure and coloration but have markedly different male genitalia and, in the case of *P. valentinae*, a differently shaped clypeus. The purpose of the present study was to compare these characters in Palaearctic and Nearctic specimens of *A. antilope* in order to clarify the taxonomic status of *A. capra*.

MATERIAL AND METHODS

Specimens examined are deposited in the collections of the Federal Scientific Center of the East Asia Terrestrial Biodiversity (FSCV) of the Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, Russia, the V.I. Vernadsky Crimean Federal University (CFUS), Simferopol, Russia, the research collection of A.V. Fateryga (CAFK), Feodosiya, Russia, and the American Museum of Natural History (AMNH). A total of 122 specimens from various regions of both North America and Eurasia were studied (see appendix). Photographs of the specimens were taken with a Canon EOS 550D digital camera and a Yongnuo YN-14EX macro flash attached to an Olympus SZ60 stereomicroscope. Focus stacking images were created using CombineZP software. The final illustrations were postprocessed for sharpness, contrast, and brightness using Adobe Photoshop CS2 software. Male genitalia were extracted after hydrating the specimens and boiling in 10% NaOH for 5 min. After that, they were rinsed in 80% ethanol and only then stored and studied in glycerin.

Species delimitation is based on the external morphology and the structure of the male genitalia. Distribution of species follows Buck et al. (2008) and Antropov and Fateryga (2017).

TAXONOMY

Ancistrocerus antilope (Panzer, 1798)

Figures 1A, 1C, 2A, 2B, 2E, 2F

Vespa insolens Harris, 1782: 129 (type locality: England; type material destroyed). Synonymized by van der Vecht and Fischer, 1972: 108. Nomen oblitum.

Vespa antilope Panzer, 1798: 9 ([♀]; type locality: "Austria"; type material destroyed). Nomen protectum.

Odynerus pictus Curtis, 1826: 137, no. 2 (type locality: Great Britain and Ireland; type material in the Melbourne Museum, Melbourne, Australia). Synonymized by Blüthgen, 1938: 284.

DIAGNOSIS: The species can be distinguished from all other *Ancistrocerus* species by the following combination of characters: female clypeus about 1.15× as wide as long in frontal view, its apical margin slightly but distinctly emarginate (fig. 1A); male clypeus about 1.2× as wide as long in frontal view (fig. 1C); anterior angles of the pronotum obtuse in dorsal view; meta-pleuron and lateral surface of the propodeum shining, impunctate, without rugosity; inferior ridge of the propodeum well developed; sternum 2 in lateral view evenly convex, in ventral view without a longitudinal furrow at base; cuspis without an additional lobe below the base of the digitus, digitus large (figs. 2A, 2B); aedeagus in dorsal view with a broad bifurcate apex (fig. 2E), in lateral view evenly curved (fig. 2F); ventral lobe of the aedeagus in lateral view with a distinct sclerotized angle at base (fig. 2F).

DISTRIBUTION: Europe (all regions), Russia (all federal districts), Turkey, Afghanistan, Kyrgyzstan, Kazakhstan, Mongolia, China (northeast), Japan (Hokkaido, Honshu), India (Kashmir).

REMARKS: Van der Vecht and Fischer (1972) reported that the name *Vespa insolens* would be proposed for permanent rejection but we did not find the corresponding proposal. Yet, to



FIGURE 1. Heads of *Ancistrocerus* species in frontal view. **A, C.** *Ancistrocerus antilope* (Panzer, 1798) from Crimea. **B, D.** *Ancistrocerus capra* (de Saussure, 1857) from New York State. **A, B.** Females. **C, D.** Males. Scale bar = 1 mm.

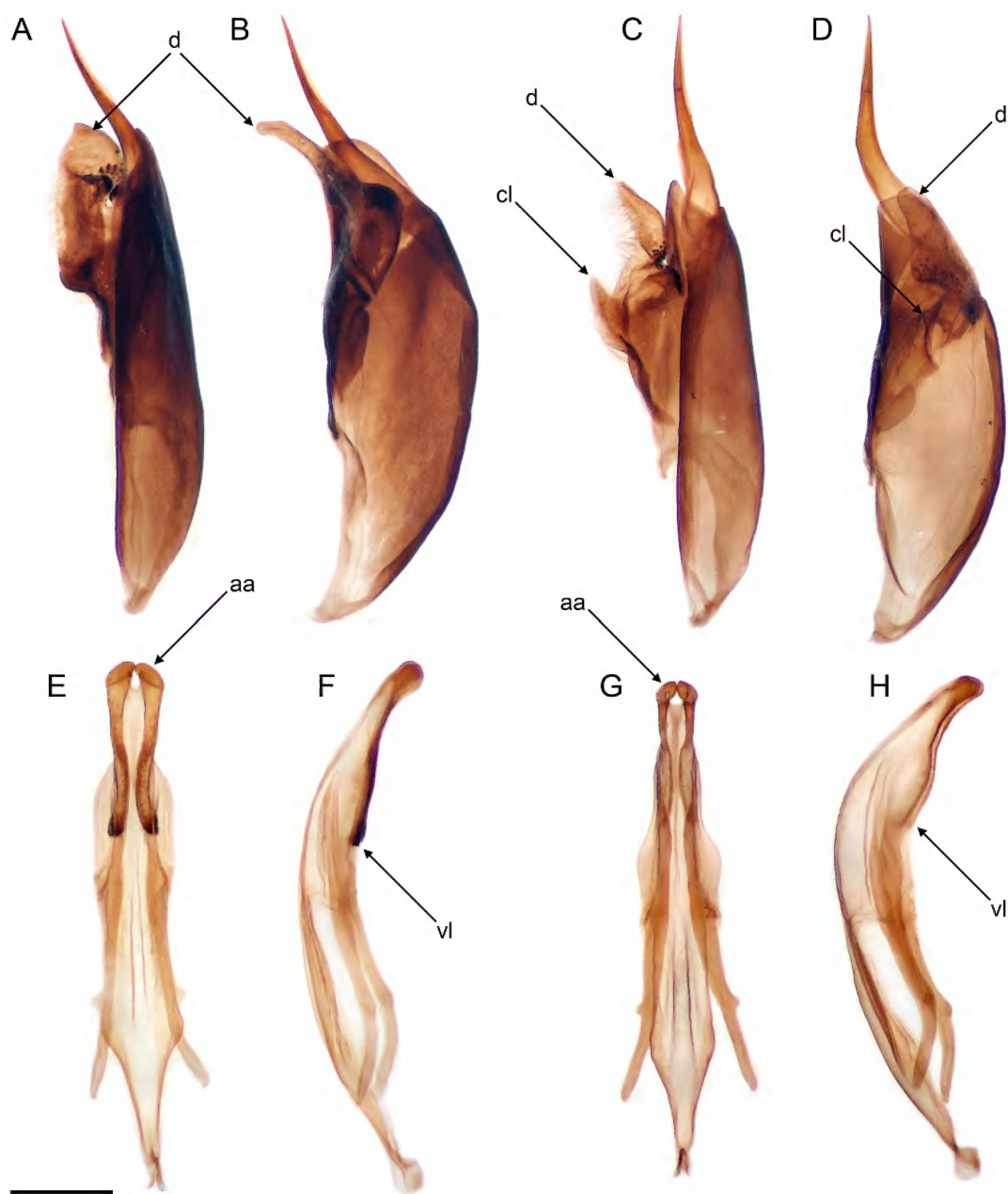


FIGURE 2. Male genitalia of *Ancistrocerus* species. A, B, E, F. *Ancistrocerus antilope* (Panzer, 1798) from Crimea. C, D, G, H. *Ancistrocerus capra* (de Saussure, 1857) from Colorado. A, C. Left paramere and volsella, dorsal view. B, D. Left paramere and volsella, medial view. E, G. Aedeagus, dorsal view. F, H. Aedeagus, lateral view. Scale bar = 0.5 mm. Abbreviations: aa = aedeagus apex; cl = cuspis lobe; d = digitus; vl = ventral lobe.

the best of our knowledge, *V. insolens* has not been used as a valid name since 1899. On the other hand, the name *A. antilope* has been used as the presumed valid name for this taxon in far more than 25 works, published by far more than 10 authors in the immediately preceding 50 years and encompassing a span of far more than 10 years (see References). According to Article 23.9.1 of the ICZN (1999), *A. antilope* is the valid name for this taxon and is considered a nomen protectum, while *V. insolens* is assigned the status of nomen oblitum.

Ancistrocerus capra capra (de Saussure, 1857), species restituted

Figures 1B, 1D, 2C, 2D, 2G, 2H

Odynerus capra de Saussure, 1857: 273 (type locality: "États-Unis et Canada" [USA and Canada]; type material in the Museum of Natural History, Geneva, Switzerland).

Ancistrocerus lecontei Cameron, 1908: 218–219 (♀ ♂; type locality: "Golden, Colorado" [USA]; lectotype, ♂ [Museum of Natural History, London, UK], designation by Bohart, 1965: 110). Synonymized with *A. antilope* by Bequaert, 1944: 274.

Ancistrocerus navajo Bequaert, 1925: 92–94 (♀ ♂; type locality: "Post Creek Canyon, Pinaleno Mountains, Fort Grant, Arizona" [USA]; holotype, ♀ [Academy of Natural Sciences, Philadelphia, Pennsylvania]). New synonymy.

Ancistrocerus antilope var. (or subsp.) *allegrus* Bequaert, 1944: 276 (♀ ♂; type locality: "Oregon: Corvallis" [USA]; holotype, ♀ [Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts]). New synonymy.

DIAGNOSIS: The species is closely related to *A. antilope* and shares with it the following combination of characters: anterior angles of the pronotum obtuse in dorsal view; metapleuron and lateral surface of the propodeum shining, impunctate, without rugosity; inferior ridge of the propodeum well developed; sternum 2 in lateral view evenly convex, in ventral view without a longitudinal furrow at base; aedeagus in dorsal view with a bifurcate apex. *Ancistrocerus capra*, however, strongly differs from *A. antilope* by the following combination of characters: female clypeus less broad, about 1.05× as wide as long in frontal view, its apical margin truncate, without distinct emargination (fig. 1B); male clypeus much narrower, about as wide as long in frontal view (fig. 1D); cuspis below the base of the digitus with an additional lobe directed medially, digitus much smaller (fig. 2C, D); aedeagus in dorsal view with apex narrower (fig. 2G), in lateral view more curved (fig. 2H); ventral lobe of the aedeagus in lateral view without a sclerotized angle at base (fig. 2H).

DISTRIBUTION: United States (most continental states except Alaska, Alabama, and Florida; needs confirmation from Arkansas, Louisiana, Mississippi, and Texas), Canada (all provinces).

REMARKS: Three subspecies of *A. antilope* were described from North America by J. Bequaert: *A. antilope navajo*, *A. antilope allegrus*, and *A. antilope spenceri*. The first one had been initially described as a species (Bequaert, 1925) but it was later reduced to subspecies (Bequaert, 1944). All three subspecies were claimed to be different from the typical *A. antilope* (i.e., *A. capra*) by coloration only (Bequaert, 1925, 1944). Transitional forms between *A. antilope allegrus* and the typical *A. capra* were reported by Bequaert (1944) from Colorado and we found such forms

among the material examined from this state. In Arizona, transitional forms between *A. antilope allegrus* and *A. antilope navajo* are known (Bequaert, 1944). We do not support subspecies based solely on different coloration within species (see Carpenter, 1987; and Fateryga et al., 2021), and thus two subspecies are here synonymized with *A. capra*. The status of the third subspecies, *A. capra spenceri*, remains unclear; a further investigation is required to ascertain its taxonomic independence since it has no intermediate forms to *A. capra capra*.

Ancistrocerus capra spenceri Bequaert, 1944

Ancistrocerus antilope var. (or subsp.) *spenceri* Bequaert, 1944: 277 (♀; type locality: “British Columbia: Kamloops” [Canada]; holotype, ♀ [Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts]).

DISTRIBUTION: Canada (British Columbia).

DISCUSSION

Ancistrocerus capra is similar and closely related to *A. antilope* but differs significantly from it by the structure of the clypeus (especially in the male) and the male genitalia. The previous synonymy of these two species was based on the impunctate and shining metapleuron and lateral surface of the propodeum, as well as the bifurcate apex of the aedeagus. These characters are shared by *A. antilope* and *A. capra* and, at the same time, they are not known in the remaining species of *Ancistrocerus*, although the aedeagus of *A. spinolae* (de Saussure, 1855), which is closely related to *A. capra*, has been not studied (Bequaert, 1925, 1944).

The bionomics of *A. antilope* and *A. capra* are also quite similar. The nesting habits of both species have been extensively studied in trap nests. The nest structure is similar (a row of larger cells with female progeny, separated by thin mud partitions, followed by a row of smaller cells with male progeny and a thick closing plug; nests with only female or male progeny also occur), both species are characterized by a positive correlation between nest cavity diameter and the prevalence of females in the progeny (Longair, 1981; Krombein, 1967; Budrys et al., 2010; Fateryga, 2013). It is also of note that both *A. antilope* and *A. capra* are associated with apparently the same species of symbiotic mites, *Kennethiella trisetosa* (Cooreman, 1942) (Sarcoptiformes: Winterschmidtidae), while these mites are often host specific. *Kennethiella trisetosa* was described from *A. antilope* in Europe (Cooreman, 1942) but was later also found on *A. capra* (reported as *A. antilope*) in North America (Cooreman, 1954; Cooper, 1955; Krombein, 1967; Cowan, 1984). The impunctate and shining metapleuron and lateral/posterior surfaces of the propodeum of these wasps serve as the acarinarium for the deutonymph stage of the mite. This species of mite was, however, occasionally recorded from *A. spinolae* as well (Cooper, 1955), although this species has slightly rugose sculpture of the metapleuron and propodeum (Buck et al., 2008). The taxonomy of the genus *Kennethiella* should be studied more carefully to ascertain whether it contains a single species, associated with all three mentioned species of *Ancistrocerus*, or two (or even three) closely related cryptic (host-specific) species.

The association of *K. trisetosa* with *A. antilope* and *A. capra* is correlated with a quite unusual mating behavior of these wasps. A pair of *A. capra* copulates several times (up to four) and each copulation is of a very long duration, 23–44 minutes on average, while the whole mating takes from a half an hour to four hours (Cowan, 1984, 1986); most mite deutonymphs are transmitted from the male to the female as the result of the mating. Moreover, a female can copulate several times, with different males (Cowan and Waldbauer, 1984). *Ancistrocerus antilope* has similar behavior (Budrienè, 2001; Budrienè and Budrys, 2007): a pair copulates 1–3 times and each copulation takes about 40–100 minutes. Multiple copulations of the females of *A. antilope* with different males were, however, not recorded (*A. Budrienè, personal commun.*).

Nevertheless, although the behavior of *A. antilope* and *A. capra* is quite similar, some clear differences in the bionomics of these species exist. Fateryga (2013) already drew attention to the difference between “Nearctic populations of *A. antilope*” (i.e., *A. capra*) and European populations of *A. antilope* in the number of generations per year and the sex ratio. In the first (summer) generation of *A. capra*, females prevail (61%–91%), while in the second (overwintering) generation, males are in the majority (67%–80%) (Fye, 1965, misidentified as *A. catskill*; Longair, 1981; Cowan and Waldbauer, 1984). By contrast, *A. antilope* has only one (overwintering) generation with a female-biased (66%) sex ratio (Fateryga, 2013). Seasonal swings in sex ratio of other eumenine wasps might be explained by seasonal changes in local competition for mates and inbreeding. If the overwintering generation tends to mate randomly but the summer generation engages in sibling mating, the observed changes in sex ratio would be expected. Heavy mortality during the winter (or a higher proportion of nests with only female or male progeny) might reduce the number of nests producing both sexes and this reduce sibling mating. However, *A. capra* does not have local competition for mates (Cowan and Waldbauer, 1984; Cowan, 1991).

Ancistrocerus capra is one of the most studied species of eumenine wasps. Numerous papers deal with various aspects of its natural history under the incorrect name *antilope* (Cooper, 1953, 1955, 1966; Medler and Fye, 1956; Krombein, 1967; Longair, 1981; Godfrey and Hilton, 1983; Cowan, 1984, 1986; Cowan and Waldbauer, 1984; Chapman and Stewart, 1996; etc.). This may lead to confusion with regard to *A. antilope*, whose biology has also been studied (Bonelli, 1989; Budrienè, 2001, Budrienè and Budrys, 2005, 2007; Budrys et al., 2010; Budrys and Budrienè, 2012; Fateryga, 2013; etc.).

ACKNOWLEDGMENTS

Mikhail Mokrousov (Nizhny Novgorod, Russia) kindly provided some important material to the first author. Maxim Proshchalykin (Vladivostok, Russia) loaned the specimens from FSCV for our study. Matthias Buck (Edmonton, Canada) carefully reviewed the manuscript and kindly improved its first version. The research was carried out within the state assignment of the Ministry of Science and Higher Education of the Russian Federation, no. 121032300023-7 (for A.F. and V.F.).

REFERENCES

- Antropov, A.V., and A.V. Fateryga. 2017. Family Vespidae. In A.S. Lelej, M.Yu. Proshchalykin, and V.M. Loktionov (editors), Annotated catalogue of the Hymenoptera of Russia, vol. 1. Symphyta and Apocrita: Aculeata. Proceedings of the Zoological Institute RAS, Supplement 6: 175–196.
- Bequaert, J.C. 1925. The genus *Ancistrocerus* (Hymenoptera, Vespidae) in North America, with partial key to the species. Transactions of the American Entomological Society 51 (1): 57–117.
- Bequaert, J.C. 1944. The North American species of *Ancistrocerus*, proper (Hymenoptera, Vespidae). Entomologica Americana 23 (1): 225–286.
- Blüthgen, P. 1938 (“1937”). Systematisches Verzeichnis der Faltenwespen Mitteleuropas, Skandinaviens und Englands. Konowia 16: 270–295.
- Boesi, R., et al. 2005. Trap-nesting *Ancistrocerus sikhimensis* (Hymenoptera: Eumeninae) in Nepal: nest structure and associates (Hymenoptera: Chrisididae; Acarina: Saprogllyphidae). Florida Entomologist 88 (2): 135–140.
- Bohart, R.M. 1951. Family Vespidae. In C.F.W. Muesebeck, K.V. Krombein, and H. Townes (editors), Hymenoptera of America north of Mexico. Synoptic catalog. Agriculture Monograph no. 2: 875–907. Washington, DC: U.S. Government Printing Office.
- Bohart, R.M. 1965. Synonymy of North American Odynerini described by Peter Cameron. Pan-Pacific Entomologist 41 (2): 107–113.
- Bonelli, B. 1989. Note sul comportamento di predazione e di nidificazione di *Symmorphus crassicornis* (Panzer) e *Ancistrocerus antilope* (Panzer). Descrizione di un nido di *Delta unguiculatum* Vill. (Hymenoptera, Eumenidae). Bollettino dell’Istituto di Entomologia “Guido Grandi” della Università degli Studi di Bologna 43: 89–97.
- Buck, M., S.A. Marshall, and D.K.B. Cheung. 2008. Identification atlas of the Vespidae (Hymenoptera, Aculeata) of the northeastern Nearctic region. Canadian Journal of Arthropod Identification 5: 1–492.
- Budrienė, A. 2001. Some aspects of mating behaviour of Eumenidae wasps (Hymenoptera). Norwegian Journal of Entomology 48 (1): 41–44.
- Budrienė, A., and E. Budrys. 2005 (“2004”). Hunting behaviour of predatory wasps (Hymenoptera: Vespidae: Eumeninae): is the distribution of stinging effort phylogenetically inherited or dependent on the prey type? Annales de la Société Entomologique de France (new ser.) 40 (3–4): 259–268.
- Budrienė, A., and E. Budrys. 2007. Comparison of mating of 10 Eumeninae wasps species with a brief review of sexual selection theories: a framework for future research. Acta Zoologica Lituanica 17 (2): 87–104.
- Budrienė, A., E. Budrys, and Ž. Nevronytė. 2004. Solitary Hymenoptera Aculeata inhabiting trap-nests in Lithuania: nesting cavity choice and niche overlap. Latvijas Entomologs 41: 19–31.
- Budrys, E., and A. Budrienė. 2012. Adaptability of prey handling effort in relation to prey size in predatory wasps (Hymenoptera: Eumeninae). Annales Zoologici Fennici 49: 58–68.
- Budrys, E., A. Budrienė, and Ž. Nevronytė. 2009. Check-list of Eumeninae wasps (Hymenoptera: Vespidae) collected in Lithuania using trap-nests. New and Rare for Lithuania Insect Species 21: 140–149.
- Budrys, E., A. Budrienė, and Ž. Nevronytė. 2010. Dependence of brood cell length on nesting cavity width in xylicolous solitary wasps *Ancistrocerus* and *Symmorphus* (Hymenoptera: Vespidae). Acta Zoologica Lituanica 20 (1): 68–76.
- Buschini, M.L.T., and T.D. Woiski. 2008. Alpha-beta diversity in trap-nesting wasps (Hymenoptera: Aculeata) in southern Brazil. Acta Zoologica 89 (4): 351–358.

- Cameron, P. 1908. A contribution towards the knowledge of the Odyneridae of the southwest of the United States. *Transactions of the American Entomological Society* 34 (3): 195–228.
- Carpenter, J.M. 1987. A review of the subspecies concept in the eumenine genus *Zeta* (Hymenoptera: Vespidae). *Psyche* 94 (3–4): 253–259.
- Carpenter, J.M., and T.R. Glare. 2010. Misidentification of *Vespula alascensis* as *V. vulgaris* in North America (Hymenoptera: Vespidae; Vespinae). *American Museum Novitates* 3690: 1–7.
- Carpenter, J.M., L. Dvořák, and K.M. Pickett. 2011. *Dolichovespula albida* (Sladen), a valid species, not a synonym of *D. norwegica* (Fabricius). *Entomologica Americana* 117 (3): 113–116.
- Chapman, T.W., and S.C. Stewart. 1996. Extremely high levels of inbreeding in a natural population of the free-living wasp *Ancistrocerus antilope* (Hymenoptera: Vespidae: Eumeninae). *Heredity* 76 (1): 65–69.
- Collins, J.A., and D.T. Jennings. 1987. Nesting height preferences of eumenid wasps (Hymenoptera: Eumenidae) that prey on spruce budworm (Lepidoptera: Tortricidae). *Annals of the Entomological Society of America* 80 (3): 435–438.
- Cooper, K.W. 1953. Biology of eumenine wasps I. The ecology, predation, nesting and competition of *Ancistrocerus antilope* (Panzer). *Transactions of the American Entomological Society* 79 (1): 13–35.
- Cooper, K.W. 1955 (“1954”). Venereal transmission of mites by wasps, and some evolutionary problems arising from the remarkable association of *Ensliniella trisetosa* with the wasp *Ancistrocerus antilope*. Biology of eumenine wasps II. *Transactions of the American Entomological Society* 80 (3–4): 119–174.
- Cooper, K.W. 1966. Ruptor ovi, the number of moults in development, and method of exit from masoned nests. Biology of eumenine wasps, VII. *Psyche* 73 (4): 238–250.
- Cooper, K.W. 1979. Plasticity in nesting behavior of a renting wasp, and its evolutionary implications. Studies on eumenine wasps, VIII (Hymenoptera, Aculeata). *Journal of the Washington Academy of Sciences* 69 (4): 151–158.
- Cooreman, J. 1942. Notes et observations sur les acariens. II. *Bulletin du Musée Royal d’Histoire Naturelle de Belgique* 18 (58): 1–12.
- Cooreman, J. 1954. Notes et observations sur les acariens. VI. Sur le genre *Kennethiella* nov. gen., parasite des Odynères du genre *Ancistrocerus* Wesmael. *Institut Royal des Sciences Naturelles de Belgique Bulletin* 30 (37): 1–10.
- Cowan, D.P. 1984. Life history and male dimorphism in the mite *Kennethiella trisetosa* (Acarina: Winterschmidtidae), and its symbiotic relationship with the wasp *Ancistrocerus antilope* (Hymenoptera: Eumenidae). *Annals of the Entomological Society of America* 77 (6): 725–732.
- Cowan, D.P. 1986. Sexual behavior of eumenid wasps (Hymenoptera: Eumenidae). *Proceedings of the Entomological Society of Washington* 88 (3): 531–541.
- Cowan, D.P. 1991. The solitary and presocial Vespidae. *In* K.G. Ross and R.W. Matthews (editors), *The social biology of wasps*: 33–73. Ithaca: Cornell University Press.
- Cowan, D.P., and G.P. Waldbauer. 1984. Seasonal occurrence and mating at flowers by *Ancistrocerus antilope* (Hymenoptera: Eumenidae). *Proceedings of the Entomological Society of Washington* 86 (4): 930–934.
- Curtis, J. 1826. *British entomology; being illustrations and descriptions of the genera of insects found in Great Britain and Ireland [etc.]*, vol. 4: 137. London: Curtis.
- Fateryga, A.V. 2013. The nest structure in four species of solitary wasps of the subfamily Eumeninae (Hymenoptera, Vespidae). *Entomological Review* 93 (3): 281–292.
- Fateryga, A.V. 2022. Revision of the *Pseudepipona herrichii*-group of the eumenine wasps (Hymenoptera: Vespidae: Eumeninae) with the description of two new species from China and Russia. *Zootaxa* 5154 (2): 101–126.

- Fateryga, A.V., M.Yu. Proshchalykin, M.M. Maharramov, and Yu.V. Astafurova. 2021. New records of solitary vespid wasps (Hymenoptera: Vespidae: Masarinae and Eumeninae s.l.) from the Nakhchivan Autonomous Republic of Azerbaijan. *Zootaxa* 5027 (1): 36–60.
- Fye, R.E. 1965. The biology of the Vespidae, Pompilidae and Sphecidae (Hymenoptera) from trap nests in northwestern Ontario. *Canadian Entomologist* 97 (7): 716–744.
- Godfrey, S., and D.F.J. Hilton. 1983. Nesting biology of solitary wasps and bees in the Eastern Township region, Quebec. *Canadian Field-Naturalist* 97 (1): 1–8.
- Harris, M. 1782. An exposition of English insects including the several classes of Neuroptera, Hymenoptera, & Diptera, or bees, flies, & Libellulae [etc.]. London: White and Robson.
- ICZN. 1999. International code of zoological nomenclature, 4th ed. London: International Trust for Zoological Nomenclature.
- Ivanov, S.P., A.V. Fateryga, and V.Yu. Zhidkov. 2019. Aculeate Hymenoptera (Hymenoptera, Aculeata) inhabiting trap nests in Crimea. *Entomological Review* 99 (2): 163–179.
- Iwata, K. 1938. Habits of four species of *Odynerus* (*Ancistrocerus*) in Japan. *Tenthredo* 2 (1): 19–32.
- Kimsey, L.S., and J.M. Carpenter. 2012. The Vespinae of North America (Vespidae, Hymenoptera). *Journal of Hymenoptera Research* 28: 37–65.
- Krombein, K.V. 1967. Trap-nesting wasps and bees: life histories, nests, and associates. Washington: Smithsonian Press.
- Krombein, K.V. 1979. Superfamily Vespoidea. In K.V. Krombein, P.D. Hurd, D.R. Smith, and B.D. Burks (editors), *Catalog of Hymenoptera in America north of Mexico*, vol. 2. Apocrita (Aculeata): 1469–1522. Washington: Smithsonian Institution Press.
- Longair, R.W. 1981. Sex ratio variations in xylophilous aculeate Hymenoptera. *Evolution* 35 (3): 597–600.
- Medler, J.T., and R.E. Fye. 1956. Biology of *Ancistrocerus antilope* in trap-nests in Wisconsin. *Annals of the Entomological Society of America* 49 (1): 97–102.
- Olszewski, P., and A.V. Fateryga. 2023. Notes on two nests of *Ancistrocerus oviventris* (Wesmael, 1836), with new records of its prey and brood parasites (Hymenoptera: Vespidae: Eumeninae). *European Zoological Journal* 90 (1): 150–155.
- Panzer, G.W.F. 1798. *Fauna insectorum Germanicae initia, oder, Deutschlands Insecten*. Heft 53. Nürnberg: Felseckerschen Buchhandlung.
- Piekarski, P.K., J.M. Carpenter, and B.J. Sharanowski. 2017. New species of *Ancistrocerus* (Vespidae, Eumeninae) from the Neotropics with a checklist and key to all species south of the Rio Grande. *ZooKeys* 718: 139–154.
- Rau, P., and N. Rau. 1918. *Wasp studies afield*. Princeton: Princeton University Press.
- Saussure, H.F. de. 1857. Nouveaux vespides du Mexique et de l'Amérique septentrionale. *Revue et Magasin de Zoologie Pure et Appliquée* (sér. 2) 9: 269–280.
- Taylor, L.H. 1922. Notes on the biology of certain wasps of the genus *Ancistocerus* (Eumenidae). *Psyche* 29 (2): 48–67.
- Vecht, J. van der, and F.C.J. Fischer. 1972. *Hymenopterorum catalogus*. Pars 8. Palaearctic Eumenidae. 's-Gravenhage: Junk.

APPENDIX

SPECIMENS EXAMINED

Ancistrocerus antilope (Panzer, 1798)

AFGHANISTAN: 1 ♀, 1 ♂: NE Zebak, Dehgul, VII-20-1973 (Kabakov) [FSCV].

CZECH REPUBLIC: 1 ♀: Dobříř-Hřeb., VI-27-1964 (Z. Padr) [FSCV].

KAZAKHSTAN: **Almaty Province:** 1 ♀: Ketmentau, Big Kyrgyzsay Natural Landmark, northern slopes, VII-24-1968 (Roshchina) [FSCV]. 1 ♀: Trans-Ili Alatau, Big Almaty Canyon, V-29-1969 [FSCV]. 1 ♀: Trans-Ili Alatau, Bolshoy Dalan Canyon, VI-5-1971 (N. Kurzenko) [FSCV]. **East Kazakhstan Province:** 1 ♀: Central Tarbagatay, 80 km S Aksuat, 1700 m, VII-13-1986 (V. Kazenas) [FSCV].

KYRGYZSTAN: 1 ♂: Tien Shan, Moldo-Too, Shavyr, VIII-20-1972 (Pek) [FSCV].

RUSSIA: **Altai Republic:** 1 ♀: Kosh-Agach Distr.: 5 km SE Chagan-Uzun, Tydtuyaryk Riv., 50°04.367'N, 88°25.193'E, 1780 m, VII-12-2016 (V. Loktionov and M. Proshchalykin) [CAFK]. 1 ♀: 15 km SE Kuray, 50°11'10"N, 88°07'04"E, VI-16-2022 (A. Fateryga) [CAFK]. 1 ♀: 15 km SE Kuray, 50°11'10"N, 88°07'04"E, VI-20-2022 (M. Proshchalykin) [CAFK]. 1 ♀: "Mars," 50°03'50"N, 88°18'45"E, VI-25-2022 (M. Proshchalykin) [CAFK]. **Amur Province:** 1 ♀: Komsomolsk-on-Amur, Silinskiy Park, VII-19-1984 (V. Mutin) [FSCV]. **Buryatia:** 1 ♀: 5 km N Naushki, Kharankhoy, VIII-3-1971 (A. Lelej) [FSCV]. 1 ♀: Vicinity of Kyakhta, VII-30-1977 (A. Lelej) [FSCV]. 1 ♀: 32 km W Selenginsk, Bolshaya Riv., VIII-9-1984 (A. Lelej) [FSCV]. **Chuvashia:** 1 ♀: Kanash Distr.: Kanash, VIII-3-2005 (Egorov) [CAFK]. **Crimea:** 1 ♀: Belogorsk Distr.: Karasevka, VI-2-1980 (V. Lavrenyuk) [CFUS]. 1 ♀: Yevpatoriya, V-19-2002 (D. Puzanov) [CFUS]. 2 ♀: Mt. Chatyrdag, on water, VI-11-2002 (A. Fateryga) [CFUS]. 1 ♀: Simferopol Distr.: Krasnopeshcherskoye, VI-8-2003 (S. Ivanov) [CAFK]. 1 ♂: Yalta, Uch-Kosh, VIII-14-2003 (A. Fateryga) [CFUS]. 4 ♀, 3 ♂: Karadag, reared from trap nest, 2005 (S. Ivanov) [CFUS]. 2 ♀, 1 ♂: Yevpatoriya, reared from trap nest, 2005 (D. Puzanov) [CFUS]. 2 ♂: Yevpatoriya, reared from trap nest, IV-29-V-3-2005 (D. Puzanov) [CFUS]. 1 ♀: Yalta Mountain-Forest Nature Reserve, pine forest, on water, VII-17-2005 (A. Fateryga) [CFUS]. 1 ♀: Crimean Nature Reserve, Zelenyy Gay Cordon, VI-5-2006 (S. Ivanov) [CFUS]. 1 ♀, 2 ♂: Yevpatoriya, reared from trap nest, 2007 (D. Puzanov) [CFUS]. 1 ♀, 2 ♂: Yevpatoriya, reared from trap nest, V-18-19-2008 (D. Puzanov) [CAFK]. 1 ♀: Alupka, VII-16-2008 (Potanin) [CAFK]. 1 ♂: Yalta Mountain-Forest Nature Reserve, Mt. Lapata, on *Cirsium arvense*, VII-7-2010 (A. Fateryga) [CFUS]. 11 ♀: "Kazarma Buzinova" [6 km SW Krasnolesye], reared from trap nest, V-19-2011 (V. Zhidkov) [CFUS]. 1 ♂: "Kazarma Buzinova" [6 km SW Krasnolesye], reared from trap nest, IV-18-2013 (V. Zhidkov) [CAFK]. 2 ♀: Zuya Forest, Opushki, V-28-VI-3-2013 (D. Puzanov) [CFUS]. 3 ♂: Vicinity of Alushta, forest near Vinogradnoye, on *Dorycnium herbaceum*, V-29-2014 (A. Fateryga) [CFUS]. **Irkutsk Province:** 3 ♀, 3 ♂: Baikal Lake, Bolshiye Koty, VIII-4-9-1983 (P. Nemkov) [FSCV]. **Mari El:** 1 ♀: Orsha Distr.: vicinity of Shuyka, VIII-31-2009 (M. Mokrousov) [CAFK]. 1 ♀: Novyy Toryal Distr.: Novyy Toryal, 56°59.765'N, 48°43.700'E, IX-2-2009 (M. Mokrousov) [CAFK]. 2 ♀: Mari-Turek Distr.: vicinity of Ruyka, 56°35.944'N, 49°53.534'E, IX-5-2009 (M. Mokrousov) [CAFK]. 1 ♀: Kilemary Distr.: Vizemyary, 56°25.904'N, 46°55.053'E, IX-14-2009 (M. Mokrousov) [CAFK]. **Mordovia:**

1 ♂: Ruzayevka Distr.: vicinity of Boldovo, VI-10-2007 (M. Mokrousov) [CAFK]. **Nizhny Novgorod Province:** 1 ♂: Tonkino Distr.: Aleshino, VII-26-2006 (M. Mokrousov) [CAFK]. 1 ♀: Tonkino Distr.: Tonkino, VII-26-2006 (M. Mokrousov) [CAFK]. 1 ♂: Vetluga Distr.: Kalinino, VIII-2-2006 (M. Mokrousov) [CAFK]. 1 ♀: Shakhunya Distr.: Shakhunya, VIII-3-2006 (M. Mokrousov) [CAFK]. 1 ♀: Vorotynets Distr.: Raznezhya, VIII-15-2006 (M. Mokrousov) [CAFK]. 1 ♀: Lyskovo Distr.: Selskaya Maza, VIII-17-2006 (M. Mokrousov) [CAFK]. 1 ♀: Dalneye Konstantinovo, VII-19-2008 (M. Mokrousov) [CAFK]. 1 ♂: Arzamas Distr.: vicinity of Morozovka, 55°26.177'N, 43°54.987'E, VI-23-2009 (M. Mokrousov) [CAFK]. 2 ♀: Shakhunya Distr.: vicinity of Syava, quarter no. 76, 57°59.774'N, 46°25.832'E, VII-15-2009 (M. Mokrousov) [CAFK]. 1 ♀: Dzerzhinsk, Svyatoye Lake, 56.213°N, 43.403°E, VII-29-2020 (M. Mokrousov and S. Kapralov) [CAFK]. **Orenburg Province:** 1 ♂: Kuvandyk Distr.: Shaytan-Tau Nature Reserve, VI-22-2017 (V. Nemkov) [CAFK]. **Primorskiy Territory:** 1 ♀: Ussuriyskiy Distr.: Suputinskiy Nature Reserve [currently Ussuriyskiy Nature Reserve], VII-29-1973 (A. Lelej) [FSCV]. 1 ♂: Anisimovka, VIII-16-1974 (A. Lelej) [FSCV]. 1 ♂: S from pass to Dalnegorsk, VIII-3-1979 (P. Lehr) [FSCV]. 2 ♀: Lazovskiy Nature Reserve, reared from trap nest, 1981 (T. Romankova) [FSCV]. 1 ♀: Ussuriyskiy Nature Reserve, VII-24-1983 (Shalagina) [FSCV]. 1 ♀: 20 km N Plastun, Dzhigitovka Riv., VII-30-1986 (N. Kurzenko) [FSCV]. 1 ♀, 3 ♂: 65 km NW Plastun, mountain pass, VII-31-1986 (N. Kurzenko) [FSCV]. 1 ♀, 1 ♂: 20 km NW Melnichnoye, Bolshaya Ussurka Riv., VIII-2-1986 (N. Kurzenko) [FSCV]. 1 ♀: Behind Manchur, IX-23-1986 (P. Lehr) [FSCV]. 2 ♂: Sikhote-Alin, pass in 12 km from Kabaniy Spring, VII-21-1987 (P. Lehr) [FSCV]. **Sakhalin:** 1 ♀: Central Expt. Sta., VII-30-1930 (Tomarikishi) [FSCV]. 1 ♀: 4 km S Dolinsk, VIII-19-2003 (A. Lelej and S. Storozhenko) [FSCV]. **Tatarstan:** 1 ♀: Naberezhnye Chelny, VIII-21-2006 (Katyshev) [CAFK]. **Tomsk Province:** 1 ♂: Verkhnevarovsk, Ob Riv., 60.4°N, VII-17-1990 (P. Lehr) [FSCV]. **Zabaykalskiy Territory:** 1 ♀: Vicinity of Molodovsk, VIII-2-1970 (N. Kurzenko) [FSCV].

Ancistrocerus capra (de Saussure, 1857)

CANADA: **Ontario:** 1 ♂: Nipigon, VIII-12-1948 (W. and J. Gertsch) [AMNH].

UNITED STATES: **Colorado:** 1 ♂: Larimer Co.: Hewlett Canyon, 6000–6500 ft, VII-7-1979 (J. Carpenter) [FSCV]. **Michigan:** 1 ♂: Marquette Co.: Diorite, VIII-5-1962 (J. and B. Rozen) [AMNH]. **Minnesota:** 1 ♀: Marshall Co.: Old Mill S.P., VIII-18-1972 (R. Wagner) [FSCV]. **Nevada:** 1 ♂: Humboldt Co.: 18 mi N Paradise Valley, Lye Creek Camp, 7500 ft, VII-7-1966 (F. P., and M. Rindge) [AMNH]. **New Mexico:** 1 ♂: Santa Fe Co.: 8 mi NE Santa Fe, Hyde State Park, 8700 ft, VII-30-1964 (F. P., and M. Rindge) [AMNH]. 1 ♂: Socorro Co.: 28 mi SW Magdalena, Bear Trap Camp, 8500 ft, VII-10-1965 (F. P., and M. Rindge) [AMNH]. **New York:** 1 ♀: Fishers, IX-10-1933 [FSCV]. 1 ♀, 1 ♂: Ulster Co.: Oliverea, 460–725 m, VIII-13-1995 (P. Gambino) [AMNH]. **North Dakota:** 1 ♂: Fargo, on *Solidago canadensis*, IX-3-1917 (O. Stevens) [AMNH]. **Utah:** 1 ♂: San Juan Co.: 7 mi W Monticello, Buckbroad Flat Camp, 8800 ft, VII-26-1960 (F. P., and M. Rindge) [AMNH]. **Wisconsin:** 1 ♂: Clark Co.: Worden Township, VII-28-1919 [AMNH]. **Wyoming:** 1 ♀, 1 ♂: Fremont Co.: 28 mi SW Lander, Louis Lake, 8600 ft, VIII-2-1962 (F. P., and M. Rindge) [AMNH].

All issues of *Novitates* and *Bulletin* are available on the web (<https://digitallibrary.amnh.org/handle/2246/5>). Order printed copies on the web from:
<https://shop.amnh.org/books/scientific-publications.html>

or via standard mail from:

American Museum of Natural History—Scientific Publications
Central Park West at 79th Street
New York, NY 10024

Ⓒ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).